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Bungarimba (Rubiaceae), a new genus distinguished from *Porterandia* and other allies

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Summary. A new genus, *Bungarimba* (Rubiaceae: Gardenieae), is described. It includes four species (one new combination, three new species) from Malesia, principally Borneo. Its distinction from *Porterandia* and other allies is supported by the results of a cladistic analysis of morphological characters representing growth architecture, vegetative morphology, inflorescence, floral and fruit characteristics, and palynology. The allies investigated include the Philippine monotypic *Sulitia*, which should be reinstated as a distinct genus, and *Atractocarpus*, which probably should be more narrowly defined around typical New Caledonian taxa than in recent studies, which have extended the concept of that genus to cover many more taxa in Australia and the Pacific.

Ridley's circumscription of *Porterandia* (Ridley 1939) included nine species, among which was *Porterandia sessiliflora* Ridl., known only from a handful of collections from Borneo (Sarawak) and Sumatra. Wong (1984, 1989) continued to use this species name, having identified two further collections from the Malay Peninsula as the same. It was then already quite clear that this taxon could be distinguished from the type species, *Porterandia anisophylla* (Jack ex Roxb.) Ridl. by a number of very contrasting features—in *P. sessiliflora* the stipules are free, the cymes are sessile, the calyx cup is glabrous and the corolla lobes are orbicular, whereas in *P. anisophylla* the stipules are fused to form a tubular sheath, the cymes are clearly pedunculate, the calyx is hairy and the corolla lobes are elongated (narrowly ovate to elliptic-lanceolate). There was, however, no review of *Porterandia* in Southeast Asia as a whole and these apparently striking differences were not further assessed.

As the cataloguing of more material from Malesia progressed, skepticism was expressed (notably by Ridsdale, pers. comm., who felt that documentation of an epiphytic or

lianescent growth habit for collections related to *P. sessiliflora* was somewhat inconsistent with the genus *Porterandia*). Somers (1988) removed five African species placed in *Porterandia* by Keay (1958) to a new genus, *Aoranthe*, in which the species all shared a number of character states that consistently distinguished them from Asiatic *Porterandia* species (see later). The application of the concept of *Porterandia* also seemed contentious for two species, *Randia tenuiflora* A.C. Sm. from Fiji and *Randia crosbyi* Burkill from Tonga, which Smith & Darwin (1988) transferred to *Porterandia* and, later, Puttock (1999) transferred to *Atractocarpus*. Puttock (1999) also remarked that the species of *Porterandia* from Malaysia should be investigated for inclusion in *Atractocarpus*.

It was within this scenario that Mr M.S. Zahid of the University of Malaya undertook a revision of *Porterandia*, during which a cladistic analysis of characters demonstrated that the species of *Porterandia* which conformed to the type, *P. anisophylla*, had a suite of distinguishing characters (or synapomorphies) which differentiated them as a group from *Atractocarpus* Schltr. & K. Krause (*sensu stricto*), and a group of three species represented by *P. sessiliflora* (Zahid 2004). At the same time, the taxonomic status of this group of three species that included *P. sessiliflora* (constituting the new genus *Bungarimba* described here), in relation to *Atractocarpus* s.s. and other apparently divergent elements within *Atractocarpus* s.l. (Puttock 1999) was investigated by the present author.

METHODOLOGY

The following taxa were selected to represent possibly diverse elements in the alliance studied (see also summary in Table 1):

1. three species of *Bungarimba* representing the new genus recognized;
2. *Atractocarpus* s.s., represented by its type species, *A. heterophyllus*;
3. *Neofranciella*, represented by its type species, *N. pterocarpon* (= *A. pterocarpon*, *fide* Puttock);
4. *Sukunia*, represented by its type species, *S. pentagonioides* (= *A. pentagonioides*, *fide* Puttock);
5. *Trukia*, represented by its type species, *T. carolinensis* (= *A. carolinensis*, fide Puttock);
6. *Atractocarpus* s.l. Group 1, comprising *A. crosbyi* and *A. tenuiflorus*;
7. *Atractocarpus* s.l. Group 2, comprising *A. macarthurii* sensu Puttock (= *Randia albituba* Val.); and
8. *Sulitia*, represented by its type species, *S. obscurinervia* (= *A. obscurinervius*, fide Puttock);
9. *Porterandia* s.s., represented by its type species, *P. anisophylla*.

Characters were studied for terminal taxa (in this case, species) using specimens from the herbaria BO, K, KEP, KLU, L, SAN, and SAR, and also fresh material and observations

Table 1. Summary of key name changes for taxa investigated (comprising *Atractocarpus* s.l., *Bungarimba* and *Porterandia*) and their taxonomic status indicated by the present study.

TAXA INVESTIGATED [1]

Bungarimba (Wong, this paper)	***Atractocarpus*** sensu Puttock (1999)	***Porterandia*** *sensu stricto (Zahid 2004)*	**Some relevant Basionyms / Synonyms** [1, 2]	**Status in present investigation**
B. kahayanensis				***Bungarimba***, distinct genus
B. papuana				***Bungarimba***, distinct genus
B. ridsdalei				***Bungarimba***, distinct genus
B. sessiliflora			*Porterandia sessiliflora*	***Bungarimba***, distinct genus
	A. heterophyllus			***Atractocarpus*** sensu stricto
	A. pterocarpon		*Neofranciella pterocarpon*	***Atractocarpus*** sensu stricto
	A. pentagonioides		*Sukunia pentagonioides*	relationship with other Pacific taxa requires study [3]
	A. carolinensis		*Trukia carolinensis*; *Trukia megacarpa*	relationship with other Pacific taxa requires study [3]
	A. crosbyi		*Porterandia crosbyi*	relationship with other Pacific taxa requires study [3]
	A. tenuiflorus		*Porterandia tenuiflora*	relationship with other Pacific taxa requires study [3]
	A. macarthurii		*Trukia macarthurii*	relationship with other Pacific taxa requires study [3]
	A. obscurinervius		*Sulitia obscurinervia*	***Sulitia*, distinct genus**
		Porterandia anisophylla		***Porterandia*, distinct genus**

[1] authorities are given in the text.

[2] for simplicity, basionyms and synonyms based on *Gardenia* and *Randia* (genera easily distinguished from the alliance of taxa here by their pollen grains in tetrads) are not given here.

[3] these taxa are, however, shown to be generically distinct from *Atractocarpus* sensu stricto, *Bungarimba*, *Sulitia* or *Porterandia*.

during fieldwork in Peninsular Malaysia and Sabah. As far as possible, scoring of character states for taxa in the *Atractocarpus* group was also checked against descriptions in Puttock (1999) and excellent field photographs of the type species, *A. heterophyllus* (Montrouz.) Guillaumin & Beauvis., and *Neofranciella pterocarpon* (Guillaumin) Guillaumin by Daniel, Irène and Christian Létocart and Jean-Marie Veillon in the website of the Association ENDEMIA ("Endémia, Faune & Flore de Nouvelle-Calédonie", http://www.endemia.nc/plante/ accessed on 1 June 2003). The character states were compiled in a dataset using DELTA Editor (Dallwitz 1980, Dallwitz, Paine & Zurcher 1999). The characters used for the cladistic analyses are listed in Table 2 and the resulting data used for the analyses are shown in Table 3.

Table 2. Characters for a cladistic analysis of *Bungarimba* and associated groups.

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1. Branch system: form of branching
1= monopodial, short (with just a few internodes)
2= sympodial and quite extensive, undergoing many orders of branching

2. Branching in relation to flowering: architecture
1= primary and lower-order branches with terminal cymes in forks and higher-order / ultimate branches with pseudo-lateral cymes at 2-node intervals
2= primary and all higher-order branches throughout with pseudo-lateral cymes at 2-node intervals
3= branches all opposite, flowering terminal to specialized lateral leafy branches

3. Branches on main stem: position
1= axillary
2= extra-axillary

4. Branch internodes: relative length
1= all adjacent internodes similar in length
2= short and longer internodes alternating

5. Stipules: fusion
1= stipules free to the base [*scoring this invalidates Character 6*]
2= stipules fused at the edges, at least in part

6. Stipular sheath: form
1= fused along most of the edges to form a slender cylindric tube with short terminal limbs
2= very slightly fused at the base, the free limbs much longer than the fused part

7. Stipule inner surface: hairiness
1= glabrous
2= hairy

8. Leaves at node(s) just below inflorescence development: extent of reduction
1= leaf pairs anisophyllous at proximal parts of branch system, but one of a pair often vestigial at ultimate branchlets
2= leaf pairs with one member vestigial at all points associated with flowering
3= all leaf pairs reduced in size along specialized flowering branch
4= leaf pairs all similar or slightly anisophyllous when associated with flowering

9. Leaf secondary veins: number
1= (9–)10–15 pairs or more
2= 5–8(–9) pairs

10. Leaf tertiary veins: distinctness
1= tertiary veins distinct in dry leaves
2= tertiary veins not visible or indistinct in dry leaves

11. Leaf surface: hairiness
1= glabrous
2= hairy (slightly to densely)

12. Bisexual or male inflorescence peduncle: length
1= peduncle typically distinct
2= peduncle indistinct, at most 1–2 mm long (inflorescence sessile-subsessile)

13. Bisexual or male inflorescence: branching
1= normal dichasial
2= primary branching dichasial, main branches becoming monochasial

14. Bisexual flower pedicels: length
1= sessile / subsessile
2= distinct, at least 2–3 mm long, sometimes much longer

15. Calyx: shape
1= obconical (cup-shaped)
2= spindle-shaped

16. Calyx outer surface: hairiness
1= hairy
2= glabrous

17. Calyx inner surface: hairiness
1= hairy
2= glabrous

18. Corolla lobe: relative length
1= shorter than tube, at most nearly as long as tube
2= equalling or exceeding the tube length

19. Corolla lobe adaxial surface: hairiness
1= hairy
2= glabrous

20. Corolla tube: length
1= less than 50 mm long, usually much less
2= 80–100 mm long

21. Corolla tube outer surface: hair type
1= fine, short flexuous, or minute hairs, not individually discernable without a lens
2= wholly covered by thick, stiff bristle-like hairs that are individually discernable without a lens

22. Corolla tube outer surface: hair coverage
1= tube surface completely obscured by hair
2= tube surface only sparsely or not covered by hair

23. Corolla throat aperture in mature open flowers: aperture size
1= wide, the aperture more than half the external diameter of the corolla tube
2= very narrow, due to development of a very thick, collar-like rim at the corolla throat, the aperture much less than half the external diameter of the corolla tube

24. Pollen aperture: diameter
1= normal, not smaller than 1/12 the grain diameter
2= tiny, only around 1/20 to 1/18 the grain diameter

25. Pollen sexine: structure and sculpturing
1= semitectate – reticulate
2= tectate – perforate
3= tectate - psilate

26. Fruit: shape
1= basically spheroidal (varying within a species to slightly broad-ovoid to broad-ellipsoid)
2= spindle-shaped (typically much narrowed, attenuating at both ends, rarely broadly spindle-shaped but still attenuated at both ends)

Table 3. Data matrix of 26 character values scored for a cladistic analysis of *Bungarimba* spp. and associated taxa.

Characters (columns) are numbered 1–26 following the list given in Table 2. The taxa (rows) are *Bungarimba*, marked **B1–B3** (*B. kahayanensis*, *B. ridsdalei* and *B. sessiliflora,* see text), and various other taxa placed in *Atractocarpus* by Puttock (1999): **A1** (*Atractocarpus s.s.*, represented by the type species *A. heterophyllus*); **A2** (*Neofranciella*, represented by *A. pterocarpon*); **A3** (*Sukunia*, represented by *A. pentagonioides*); **A4** (*Trukia*, represented by *A. carolinensis*); **A5–A6** (*Atractocarpus s.l.*, group 1 represented by *A. crosbyi* and *A. tenuiflorus*); **A7** (*Atractocarpus s.l.*, group 2 represented by *A. macarthurii* sensu Puttock); **A8** (*Sulitia*, represented by *A. obscurinervius*); and *Porterandia*, marked **P** (represented by the type species, *P. anisophylla*).
The outgroup comprised A1, A2, A3, A4, A5, A6, A7, A8, and P in one analysis, and P alone in another analysis. A dash (–) indicates scoring was not applicable for that character, whereas the symbol "?" indicates character states not known (i.e., missing data).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**
1 (B1)	2	2	1	1	1	–	1	2	2	2	1	2	2	1	1	2	2	1	2	1	1	1	2	1	1	1
2 (B2)	2	2	1	1	1	–	1	2	2	2	1	2	2	1	1	2	2	1	2	1	1	2	2	1	1	1
3 (B3)	2	2	1	1	1	–	1	2	2	2	1	2	2	1	2	2	2	1	2	1	1	1	2	1	1	1
4 (A1)	1	3	2	1	1	–	1	3	1	2	1	2	1	1	1	2	1	1	2	1	1	2	2	?	?	2
5 (A2)	1	3	2	1	1	–	?	3	1	?	2	2	1	1	1	1	?	2	2	1	1	2	?	?	?	2
6 (A3)	?	?	1	1	1	–	?	?	1	1	1	1	?	2	1	?	?	2	2	1	1	2	?	1	2	2
7 (A4)	2	2	1	1	2	1	?	4	1	1	1	1	2	2	1	2	?	2	2	1	1	2	2	1	1	1
8 (A5)	2	2	1	1	2	2	?	4	2	1	1	2	2	2	1	1	1	2	2	1	1	2	2	?	?	1
9 (A6)	2	2	1	1	2	2	?	4	2	1	1	1	2	2	1	?	?	2	2	1	1	2	2	?	?	1
10 (A7)	2	2	1	1	2	1	2	4	1	1	1	1	2	2	1	2	1	2	2	1	1	1	2	?	?	1
11 (A8)	2	2	1	2	2	2	?	2	1	1	1	2	2	1	1	?	?	1	2	2	1	2	?	2	3	2
12 (P)	2	1	1	1	2	1	2	1	1	1	2	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1

For the cladistic analyses, characters were polarized by the outgroup method. Two separate analyses were carried out. One used all nine taxa other than the three species of *Bungarimba* as outgroup (i.e., leaving only *Bungarimba* as ingroup). The second used only *Porterandia anisophylla* as outgroup (i.e., considering *Bungarimba* and other related taxa as an alliance, the ingroup, the members of which were more similar to one another than to *Porterandia*). The programme PAUP (Version 4.0 beta version, Swofford 1998) was used for the cladistic analyses. An exhaustive search was possible in view of the relatively small number of taxa involved and in each analysis, a total of 654 729 075 trees were evaluated. Tree scores ranged from 41 to 79 and in each of the analyses, a single output tree was retained with the best score of 40, consistency index of 0.73 and retention index of 0.77. These output trees from PAUP were viewed and rooted using the programme TreeView (Win32) based on Page (1996) and transferred into MacClade 3.08a (Maddison & Maddison 1999) for character exploration.

DISTINGUISHING CHARACTERS

The taxa in the alliance analysed here (*Bungarimba*, *Porterandia*, *Atractocarpus* s.s. and the other taxa included in *Atractocarpus* s.l.) have typical characters of the Gardenieae (Robbrecht & Puff 1986): 5-merous corollas, 2-carpellate ovaries with numerous ovules in axile placentation, somewhat large fruits with slightly flattened, rounded to reniform seeds with a conspicuously long hilum, embedded in a pulp-like placenta, and porate pollen grains. In addition, they differ from other groups of the Gardenieae by a number of easily perceived characters: they are non-spiny plants which do not develop any extremely condensed specialized flowering shoots, have flowers with hypocrateriform corollas, and included anthers.

The African *Aoranthe* has been convincingly demonstrated (Somers 1988) to differ by its coloured (pale yellow, pink or reddish) corolla, its lobed floral disc, mostly tricolporate pollen and irregularly angular seeds. In contrast, *Porterandia* s.s. has creamy-white corolla, an entire floral disc, mostly triporate pollen and distinctly rounded-reniform, flattened seeds, confirmed through the studies of Zahid (2004). In addition, while Somers could only find bisexual flowers in *Aoranthe*, Zahid (2004) has confirmed gynodioecy (bisexual and female inflorescences on separate trees) and occasional gynomonoecy (bisexual and female inflorescences on the same tree) for *Porterandia*. Geographically, *Porterandia* defined in the strict sense occurs only in Southeast Asia. All species of these two genera have coarse, bristle-like hairs densely covering their corolla tubes, which impart some superficial resemblance between them (Somers 1988) but at once distinguish *Aoranthe* and *Porterandia* from the other so-called close allies, which have fine, minute hairs, if any, on the outside of the corolla tube. Somers (1988) also pointed out that *Aoranthe* appears to have more affinity to the Isertieae than the Gardenieae because its species are characterized by small angular seeds with a short hilum and fine, rib-like thickenings on the outer tangential cell walls of the exotesta, features atypical of the Gardenieae but found in the former tribe.

Bungarimba compared with *Porterandia* and *Atractocarpus* s.s.

When compared only with the remaining Australian-Malesian taxa, *Porterandia* (with 22 species) stands out through a combination of consistent defining characters (Zahid 2004). It is distinguished from *Bungarimba* and *Atractocarpus sensu stricto* (typified by *A. heterophyllus*) by its stipules which are fused into a tubular sheath, its hairy leaves, the corolla lobes which are hairy on the inner surface. Both *Bungarimba* and *Atractocarpus* s.s. have free stipules that appress together, each with one edge overlapping onto the other stipule, forming a slightly twisted structure, glabrous leaves, and corolla lobes that are glabrous on the inside surface.

Moreover, these three taxa have very different architectural features related to their branching and flowering, although in all, primary branches basically arise from the orthotropic axis (vertical main shoot) as opposite and decussate pairs, from the axils of normal leaf-pairs (Fig. 1). In *Porterandia*, the primary branch forks at intervals, each fork formed by a pair of axillary branches that contain either an inflorescence or dormant or aborted terminal bud in the angle between them. Such forks occur successively with an odd number of internodes (usually 3, 5, or 7, at times just 1 or 9 internodes) between them, are abundant, conspicuous and typical of the proximal portions of branch systems. The distal portions of the finer branches, at the edge of the crown, however, often bear inflorescences at intervals of two internodes: here, the inflorescence (still terminal) is pushed to a lateral position by sympodial development of a relay axillary branch from the final node preceding it.

In *Bungarimba*, both primary and higher-order branches bear inflorescences at 2-internode intervals, rather regularly. The inflorescences are also terminal, but become pushed to one side (the upper side of the branch) by the sympodial development of a relay axillary branch from the final (second) node of each branch segment. The inflorescences thus occur at 2-internode (or 2-node) intervals, and along a typical portion of the branch system this resembles development of inflorescences after every two internodes, on the upper side only, along a reasonably straight axis, which is in fact a sympodium. Pairs of axillary branches also develop occasionally, from the axils of a leaf pair held in the (sub-)horizontal plane and which alternates with the so-called flowering node; such pairs of branches will then contain a branch axis between them.

Thus in *Porterandia*, forks are common in the primary architecture of the plant, and the forks are associated with inflorescences between them; whereas in *Bungarimba*, such forks are uncommon and inflorescences are, as a rule, found after every two internodes along the branch system. Also, in *Bungarimba*, every node immediately below the inflorescence (i.e., the uppermost node in a 2-internode segment) has one leaf completely undeveloped; this is not the case in *Porterandia*, where terminal inflorescences associated with branch forks arise immediately after a pair of sometimes slightly anisophyllous leaves, and

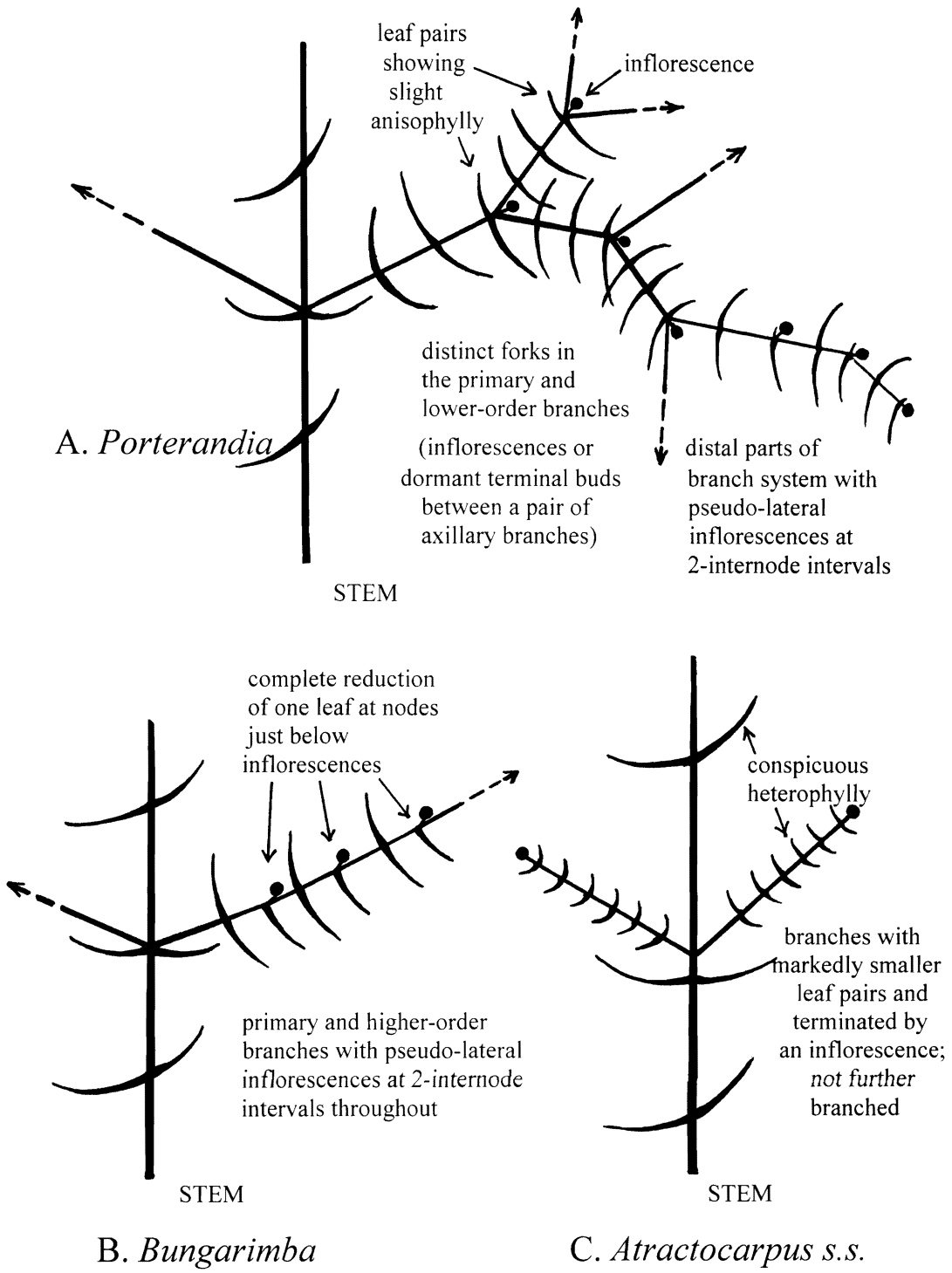
leaf pairs showing slight anisophylly
inflorescence
distinct forks in the primary and lower-order branches
(inflorescences or dormant terminal buds between a pair of axillary branches)
distal parts of branch system with pseudo-lateral inflorescences at 2-internode intervals
A. Porterandia
STEM
complete reduction of one leaf at nodes just below inflorescences
primary and higher-order branches with pseudo-lateral inflorescences at 2-internode intervals throughout
STEM
B. Bungarimba
conspicuous heterophylly
branches with markedly smaller leaf pairs and terminated by an inflorescence; not further branched
STEM
C. Atractocarpus s.s.

Fig. 1. Branch architecture in relation to flowering (inflorescence production) compared for *Porterandia* (A), *Bungarimba* (B) and *Atractocarpus* s.s. (C).

inflorescences are only associated with complete suppression of one leaf of a pair where they occur at 2-internode intervals at the distal portions of branchlets.

These represent rather different patterns of branching and flowering development. In the type species of *Atractocarpus* (*A. heterophyllus*) the inflorescences are terminal to axillary branches that bear leaves of a much-reduced size (up to about a fifth the length of normal foliage leaves: hence the specific epithet). Here the inflorescence development is associated in a different way with leaf reduction and sympodial branch development does not proceed from these specialized inflorescence-terminated branches. Also, these specialized branches develop in an extra-axillary position on the main stem, another feature not found in *Bungarimba* and *Porterandia*.

Bungarimba compared with other Malesian and Pacific taxa

The new genus *Bungarimba* is also distinguishable from many of the other species placed in *Atractocarpus* (*non sensu stricto*) by Puttock (1999). Many of these may not be sufficiently understood but most also differ from the type species *A. heterophyllus* in the mode of inflorescence production. It is clear from descriptions and figures provided by Puttock (1999) that nearly all of these have "binodal" branch segments with inflorescences produced after every two internodes, thus differing substantially from the type, described above. Also, several characters investigated for the present work have not been studied for their distribution in *Atractocarpus sensu* Puttock in the paper by Puttock & Quinn (1999), on which was based the new circumscription of *Atractocarpus* in Puttock (1999). For example, the calyces in *Bungarimba* are always glabrous within; those in *Porterandia* (and also the African *Aoranthe*) are invariably hairy inside, as are the calyces of a number of species placed in *Atractocarpus* for which Puttock has provided notes on this character (for a number of other species pubescence within the calyx was not commented upon). When Puttock & Quinn (1999) carried out their analysis (their "data sets 2 and 3" and Figs. 2 and 3), a sizeable number of taxa were unresolved although they came out nested within a clade considered the "*Atractocarpus* clade" (the authors commented that "the entire clade is well supported. . .there is virtually no internal topology that is supported in terms of either parjack or decay"); yet a number of the characters discovered to be important in distinguishing *Porterandia* and allies were not surveyed for that analysis.

It is, however, true that the performance of a cladistic analysis can be strongly influenced by the selection and resolution of taxa and characters (Kitching et al. 1998). Thus, if taxonomically important characters are missed out from a survey, taxa may segregate to or cluster at different levels than they might otherwise, affecting decisions on relationships.

Likewise, other small Pacific genera subsumed under *Atractocarpus* in the scheme of Puttock (1999) also have substantial differences from the group of three species that constitute the new genus *Bungarimba*. *Neofranciella* Guillaumin is typified by the New Caledonian *N. pterocarpon* (= *A. pterocarpon* (Guillaumin) Puttock), with specialized

flowering leafy branches produced in extra-axillary position as in *Atractocarpus heterophyllus*, also of New Caledonia, although it also has a strongly ridged fruit (taken by Puttock as of specific significance only: a species autapomorph). *Neofranciella* and *A. heterophyllus* also share an elongate (spindle-shaped) fruit shape, quite different from the fundamentally spherical fruit shape in *Bungarimba* or *Porterandia*; this would be a notable synapomorphy for these two closely related taxa. Specialized extra-axillary branches that bear reduced leaves and terminal inflorescences and elongate fruits are also found in at least two other New Caledonian species, *A. platyxylon* (Veill. ex Pancher & Sebert) Guillaumin and *A. simulans* Guillaumin, so that these characters probably represent a series of synapomorphies for taxa in the close alliance of *A. heterophyllus*, the type species of *Atractocarpus*. Puttock (1999) does not discuss these other species.

Trukia Kaneh. is typified by the Micronesian *T. megacarpa* (Kaneh.) Kaneh. (= *T. carolinensis* (Val.) Kaneh. & Hatus. or *A. carolinensis* (Val.) Puttock), which has fused stipules, distinct leaf tertiary venation, pocket-domatia in the leaf-vein axils, distinctly pedunculate inflorescences and rugulose fruit with pale-scurfy exocarp, all of which are also characteristic of the New Guinean *A. macarthurii* (sensu Puttock). In contrast, *Bungarimba* spp. have free stipules, indistinct to invisible leaf tertiary venation and no pocket-domatia, sessile inflorescences and smooth fruit.

Sukunia A.C.Sm. is another such small Pacific genus. Its type species, *S. pentagonioides* (Seem.) A.C.Sm. (= *A. pentagonioides* (Seem.) Puttock), *S. longipes* A.C.Sm. (= *A. longipes* (A.C.Sm.) Puttock) (both from Fiji), and the two taxa once placed in *Porterandia* by Smith & Darwin, *Randia tenuiflora* (= *Atractocarpus tenuiflorus* (A.C.Sm.) Puttock, from Fiji) and *Randia crosbyi* (= *Atractocarpus crosbyi* (Burkill) Puttock, from Tonga) also differ from *Bungarimba* in a number of characters. These include distinct leaf tertiary venation, long-pedicellate flowers, and corolla lobes equaling to longer than the tube. *Bungarimba* spp. as a group are well distinguished by their indistinct leaf tertiary venation, subsessile flowers, and corolla lobes shorter than, or at most approaching the length of, the tube.

Finally, the monotypic Philippine *Sulitia obscurinervia* (Merr.) Ridsdale (= *A. obscurinervius* (Merr.) Puttock) has some resemblance to *Bungarimba* in that every node immediately below the inflorescence, which develops after every two branch internodes, has one leaf completely undeveloped (Ridsdale 1979); however, it differs in its alternating long and short internodes along the branch, very long (8-10 cm) corolla tube with linear lanceolate lobes 3–5 cm long. The pollen of *Sulitia obscurinervia* has a psilate (tectate) exine (see pollen photographs in Fig. 21 d & e in Robbrecht & Puff 1986), with very small apertures that do not have any annular rim-thickenings. In contrast, the pollen of *Bungarimba* and many of the other species placed in *Atractocarpus* by Puttock (1999) have reticulate (semitectate) or perforated (tectate) exine, and the apertures are bigger, mostly with annular rim-thickenings. Puttock & Quinn (1999) score pollen characters for *Sulitia obscurinervia* as "unknown" (see their Table 1) although in the generic description of

Atractocarpus (which includes *Sulitia*) (Puttock 1999) the pollen exine is described as reticulate. These characters continue to support the status of *Sulitia* as a rather unique genus, monotypic and restricted to the Philippines.

Some characters seem of potential importance from a general survey, but require complete documentation for more taxa. For example, Puttock (1999) documents the calyx as "hispid" for *N. pterocarpon* (as *A. pterocarpon*) and "densely pubescent inside" for *A. macarthurii* but does not comment on the character of calyx pubescence for other taxa mentioned here. The inner surface of the calyx is hairy in *A. heterophyllus* (type species of *Atractocarpus*), as verified with *Stone* 14916, New Caledonia, Isle of Pines (KLU!). In contrast, *Bungarimba* spp. are characteristically glabrous inside the calyx. Still other characters remain to be better surveyed and understood. The epiphytic and hemi-epiphytic growth forms seem generally better developed among taxa in the Malay Archipelago and Southwest Pacific region, where rainfall is higher and conditions moister, compared to more seasonal territories, such as on mainland Southeast Asia (Whitmore 1998). In all three species of *Bungarimba*, the male or bisexual inflorescences, which are multi-flowered, have cyme branches that develop monochasially, so that each of several main cyme branches become a sub-helicoid structure with condensed internodes and flowers arranged on the upper side of the branch. This kind of inflorescence seems to produce flowers over a prolonged period, at least beyond the development period of one to several sympodial branch segments. Puttock (1999) notes this for a number of species he places in *Atractocarpus*; he says, "some inflorescences may continue flowering long after the branch has developed, perhaps for several seasons, giving the appearance of cauliflory..." Certainly this is not the case in *Porterandia* (Zahid 2004) but to what extent such a character may be linked to adaptation and evolution within a generally archipelagic setting is unknown.

INFERENCES FROM THE CLADISTIC ANALYSES

In our analysis that considered only *Bungarimba* spp. as the ingroup, the sole output tree (Fig. 2) identified the three *Bungarimba* spp. as a monophyletic clade for which the glabrous calyx inner surface was a clear synapomorphy. Among the outgroup taxa, the pair of *A. heterophyllus* and *Neofranciella pterocarpon* (both New Caledonian taxa) emerged as another monophyletic clade supported by at least four synapomorphies (extra-axillary branching, short monopodial branches, flowering terminal to specialized lateral leafy branches, and all leaf pairs along specialized flowering branches reduced in size). Among the remaining outgroup taxa, only *Sulitia obscurinervia*, *Sukunia pentagonioides* and *Porterandia anisophylla* were clearly marked by apparent autapomorphies. *Sulitia obscurinervia* (sole species of a monotypic genus) had as many as four autapomorphies (alternating short and long branch internodes, very long corolla tube, very tiny pollen apertures, psilate pollen sexine), and *Porterandia*, five (branches mostly with terminal cymes in forks, leaf pairs anisophyllous at proximal parts of branch system, corolla lobe

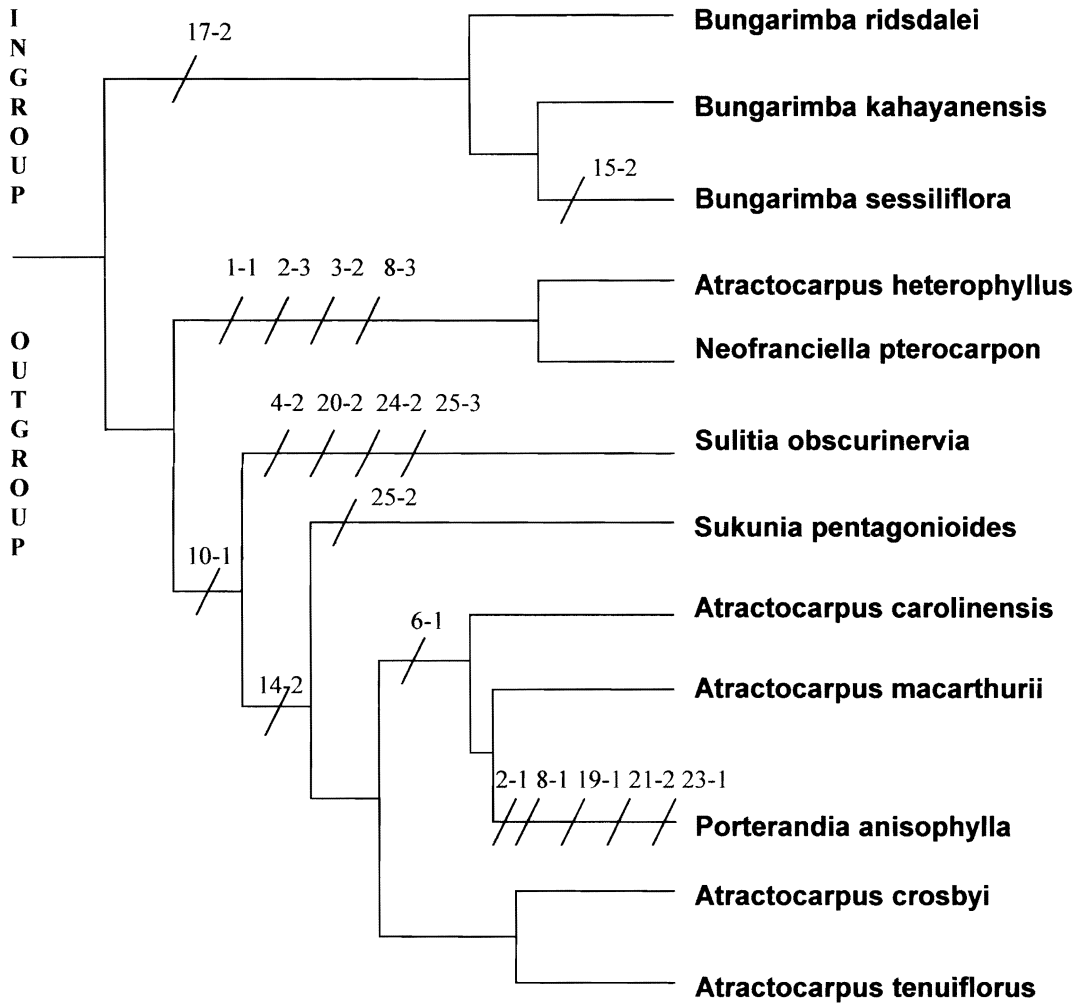

Fig. 2. The sole output tree (40 steps) generated from an exhaustive search in a cladistic analysis of *Bungarimba* spp. with representatives of their closest allies all forming the outgroup. Identified synapomorphies are noted along branches, their numbering corresponding to character states listed in Table 2.

adaxial surface hairy, corolla tube wholly covered by stiff bristle-like hairs, wide corolla throat aperture). The five autapomorphies for *Porterandia anisophylla* here are in fact synapomorphies for all species of *Porterandia* identified in the revision by Zahid (2004). Thus, these two taxa (*Sulitia* and *Porterandia*) appear to be very well-differentiated and may be considered equivalent to the *A. heterophyllus* - *Neofranciella* clade identified in Fig. 2.

In the other analysis that used only *P. anisophylla* as the outgroup (i.e., treating *Bungarimba* and its allies except for *Porterandia* as the ingroup), the same implications appeared. The sole output tree (Fig. 3) illustrates this. The outgroup taxon, *Porterandia anisophylla* was

clearly distinguished. Among the ingroup taxa, all three species of *Bungarimba* segregated as a clade (unified by the glabrous calyx inner surface), as did the pair of *A. heterophyllus–Neofranciella*, which was distinguished by the synapomorphies mentioned above. *Sulitia obscurinervia* was well distinguished by four autapomorphies, while *Sukunia pentagonioides* was segregated by the autapomorphous character of perforate pollen grains.

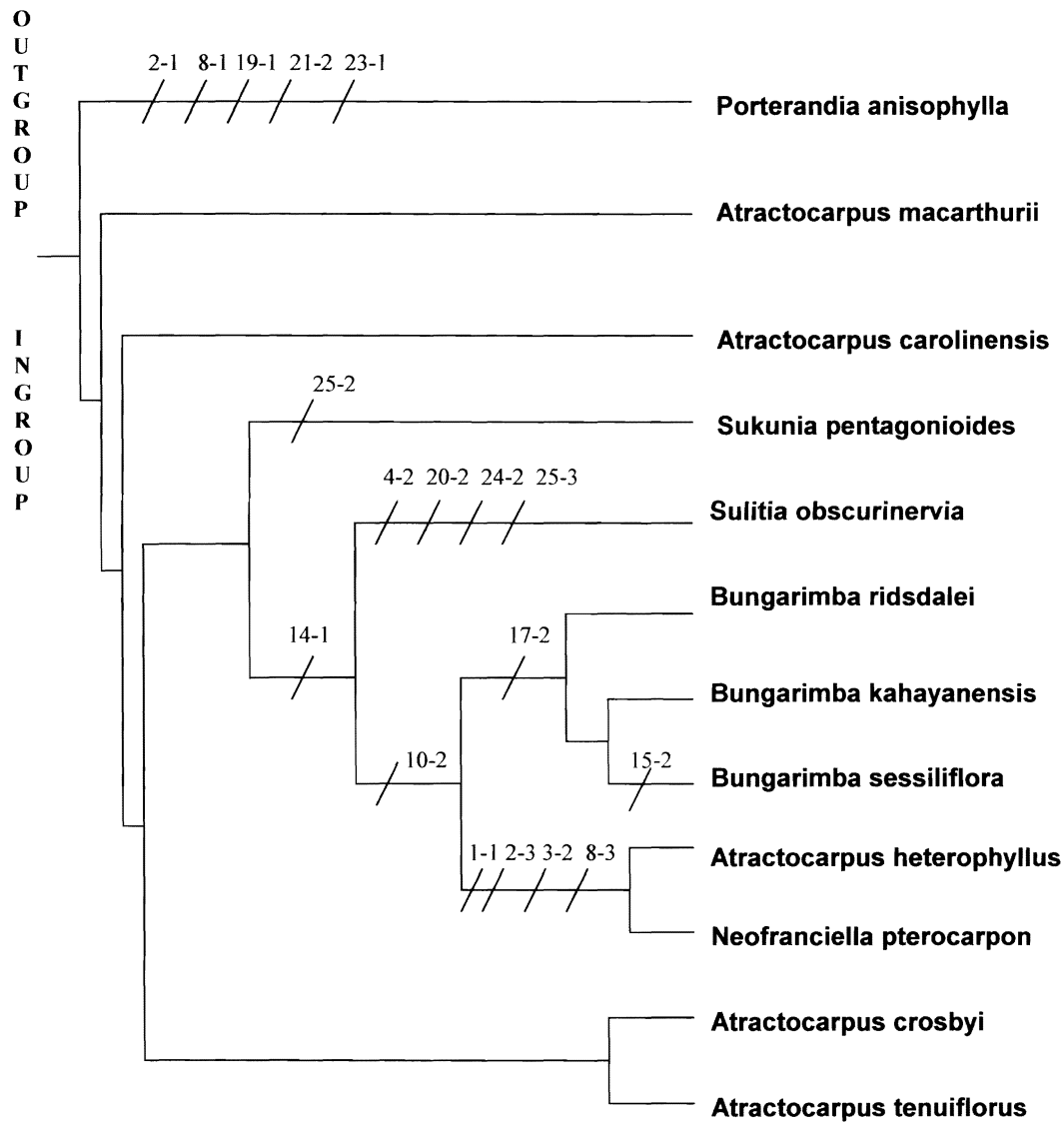

Fig. 3. The sole output tree (40 steps) generated from an exhaustive search in a cladistic analysis of *Bungarimba* and its closest allies, with *Porterandia anisophylla* as the outgroup. Identified synapomorphies are noted along branches, their numbering corresponding to character states listed in Table 2.

The remaining taxa, *Atractocarpus macarthurii*, *A. crosbyi*, *A. tenuiflorus* and *A. carolinensis* were not specially resolved, although these were sufficiently distinguished from *Atractocarpus* s.s. (including *Neofranciella*), *Bungarimba*, *Sukunia* and *Sulitia*.

The cladistic analyses therefore support the concepts of *Atractocarpus* s.s., *Bungarimba* and *Sulitia* as distinct genera, and suggest that poor resolution of (i.e., lack of a clear topology for) a number of other taxa placed within *Atractocarpus* s.l. does not permit their interpretation as members of any coherent grouping, although they are sufficiently distinguished from *Atractocarpus* s.s. itself. As *Sukunia pentagonioides* is marked by only an apparent autapomorphy in the present analyses, its distinction as a genus is still difficult to interpret without further comparison with the many other species of *Atractocarpus* s.l.

The present paper, therefore, proposes the reinstatement of *Sulitia* (as a monotypic genus from the Philippines) and recommends a narrower definition of *Atractocarpus* (that also includes *Neofranciella*), while maintaining that more complete studies of a whole host of related Southwest Pacific and Australian taxa are required for their appropriate taxonomic placement. The distinctness of *Bungarimba* as a genus is also supported by the analyses.

BIOGEOGRAPHICAL CONSIDERATIONS

With a landscape fragmented into numerous islands spanning the Malesian-Australian region, it is not surprising to find a significant number of endemic genera occurring, although it is a fact that some of these are proving not to be distinct from other more widespread genera (Johns 1995, Wong 1998). Such "small" genera of limited distribution may be very distinct taxa or may form complexes which (theoretically, at least) represent terminal taxa that are apparently reticulately linked by different characters.

Within the flora of this region, including large families such as the Rubiaceae, are many little-known taxa, for which general and superficial assessment may not have revealed sufficiently understood group characters for their consistent recognition. It is implied that in such cases where discovery of a fairly comprehensive range of characters may have been hampered, cladistic analysis of characters more generally documented for other taxa may not bring satisfactory resolution.

The three species of *Bungarimba* analysed above, together with a fourth, incompletely known species found in New Guinea, define a genus centred on Sundaland. This genus is sufficiently distinguished by a number of morphological characters from *Porterandia*—here understood also as Sundaland-centred (Zahid 2004)—as well as *Atractocarpus* and various other genera found mostly in the Australasian-Southwest Pacific region and the Philippines.

THE NEW GENUS

Bungarimba *K.M.Wong* **genus novum** *Rubiacearum, corolla hypocrateriformi, staminibus tubo corollae affixis et inclusis, ovario inferiore biloculare placentatione axiali Porterandiae Ridley et generibus cognatis affinis sed nodiis infra inforescentiis unifoliosis, stipulis usque ad basin liberis, foliis glabris, in sicco nervulis indistinctis vel invisibilibus, ramulis inflorescentiae habitu monochasiali, tubis calycis extus et intus glabris differt. Typus: Bungarimba sessiliflora (Ridley) K.M.Wong*

Porterandia Ridley, *pro parte*, Kew Bulletin (1939) 593–597, Wong, Malayan Nature Journal 38 (1984) 1–57 *et* Tree Flora of Malaya 4 (1989) 392–393 *quoad P. sessiliflora*; Coode *et al.*, Checklist of Flowering Plants & Gymnosperms of Brunei Darussalam: 285–286 *quoad P.* sp. 1 (Wong 1340); *non Porterandia* Ridley *sensu typica.*

The genus name is composed from two words in the Malay language, *bunga* (= flower) and *rimba* (= rain forest).

Polygamous trees, epiphytes or hemi-epiphytes developing fine adventitious roots and thick aerial roots that reach the forest floor. **Primary branching** opposite and decussate, each branch then developing as a sympodial relay system with 2-internode (or binodal) branch segments, each segment typically with a proximal node bearing a pair of normally developed leaves in a (sub-)horizontal plane and a distal node bearing a single developed leaf on the lower side of the node opposite to a totally reduced member on the upper side of the node (often held in a subvertical plane); with inflorescence development basically terminal to each 2-internode branch segment and typically developing immediately distal to the 1-leaf node, but pushed to a lateral position on the upper side of the branch by growth of a new branch from the leaf axil on the lower side of the branch which continues the sympodial relay, thus forming a lateral branch along which alternate nodes bear only a single leaf on the lower side of the branch and inflorescences develop only at such nodes but on the upper side of the branch; the inflorescence rarely and atypically terminating the shoot immediately after a fully-formed pair of leaves. **Additional branching** along sympodial relay branches typically as divergent solitary or paired branches at 2-leaf nodes with the parent relay-axis continuing as a central axis, typically and rarely as paired divergent branches with the inflorescence in the fork. **Stipules** 2, ovate-elliptic-lanceolate, free to the base, each with one edge overlapping onto the opposite stipule, the apical portion slightly twisted, glabrous. **Leaves** elliptic-ovate, coriaceous, glabrous, with few (up to 8–10) pairs of secondary veins, finer venation obscure. **Inflorescence** fundamentally a sessile to subsessile cyme; in the male and bisexual with several to many (more than 5) orders of branching, the lower branches dichasially formed, these becoming monochasial and (sub)helicoid (apparently extending and bearing flowers over a prolonged duration even as subsequent shoot development produces more inflorescences); in the female unbranched, or occasionally branched just once, bearing 1–2 flowers. **Flowers** male, bisexual or female

(apparently often on separate individuals, but sometimes male or female inflorescences occurring together with bisexual inflorescences on the same branch or individual); calyx spindle-shaped to cup-shaped, glabrous outside and inside, lobes 5, irregularly shaped or rounded, minutely ciliate on the margin; corolla hypocrateriform, the tube cylindrical or slightly broadened at the upper part, outside scantily to densely covered with minute, fine hairs, inside glabrous or hairy at the basal portion, the throat developing a thick collar of tissue that constricts the aperture of the tube to less than half the throat diameter, the lobes 5, overlapping to the left, suborbicular to narrowly ovate to elliptic, shorter than or nearly as long as the tube, outside sparsely to densely minute-hairy, inner surface totally glabrous; anthers sub-medifixed just above the middle of the corolla tube, reaching up to just below the corolla throat and entirely included, pollen-bearing in male and bisexual flowers, dehiscing in an advanced stage of the flower bud (the bisexual flowers thus protandrous) and releasing pollen lodged onto the stigmatic surface and subsequently so presented when the corolla opens, empty in female flowers; style totally glabrous, stigma 2-lobed, surface lightly grooved; disc annular, not lobed; ovary 2-locular, developed in the female and bisexual flower, failing in the male flower; ovules many, placentation axile. **Fruit** subglobose to obovoid, glabrous, 2-locular, generally more than 1 cm long when mature; seeds lens-shaped to reniform, somewhat compressed, testa surface areolate.

KEY TO *BUNGARIMBA* SPECIES

Mature fruit pedicels 1–1.5 cm long ..... **2. *Bungarimba papuana***

Mature fruit pedicels not more than 0.5 cm long

Corolla tube and lobes with scattered, minute hairs or subglabrous on the outside ..... **3. *Bungarimba ridsdalei***

Corolla tube and lobes densely covered by pale, minute hairs on the outside

Calyx spindle-shaped, with a tiny aperture, the limb torn irregularly by the developing, expanding corolla; corolla lobes short-ovate to suborbicular, less than half the length of the corolla tube ..... **4. *Bungarimba sessiliflora***

Calyx obconical, with a wide mouth; corolla lobes narrowly ovate to elliptic, more than half the length of the corolla tube ..... **1. *Bungarimba kahayanensis***

ENUMERATION OF SPECIES

In specimen listings in the following enumeration, the sexual states of material, where determinable, are designated by *B* (bisexual), *M* (male), *F* (female), and where indeterminate, *X* (sex not interpretable, including specimens with only vegetative material).

1. Bungarimba kahayanensis K.M.Wong, **sp. nov.** *B. sessiliflorae (Ridl.) K.M.Wong affinis corolla externe sparse puberula differt. Typus: Burley, Tukirin et al. 772, C. Kalimantan, headwaters of S. Kahayan, 5 km NW of Tumbang Sian logging camp, 150 m, 21 April 1988 (holotypus SAR! isotypi K! KEP! L! SING!).*

(Fig. 4.)

Epiphyte or hemi-epiphyte at 7 m high or more, occasionally a terrestrial shrub. **Bark** smooth, pale brown. Shoots and leaves glabrous. **Stipules** ovate-lanceolate, free, each with one edge overlapping onto the other, to 1.5 cm long, the whole slightly twisted, glabrous. **Leaves** with petiole 0.7–2.4 cm long, 1.5–2 mm thick; lamina narrowly to broad-elliptic to obovate, 6.5–20 cm long, 3.2–9.4 cm wide, base cuneate to rounded, apex acute, cuspidate or caudate, coriaceous; midrib on the upper surface slightly prominent, on the lower surface conspicuously prominent; secondary veins 5–8 pairs, slightly prominent on the upper side, prominent on the lower side; tertiary veins indistinct in the dried leaf. **Bisexual and male inflorescences**: peduncle 0–1 mm long, compactly branched several to more than 5 times, the main branches subsequently monochasial and sub-helicoid with highly condensed internodes and broad-ovate bracts less than 1/3 the length of the flower calyx; flowers (known only in the advanced bud stage) typically more than 8 in a cyme, pedicels 0.5–1 mm long, 1–1.5 mm thick; calyx cup-shaped, glabrous outside and inside, lobes 5, rounded, to 0.5 mm high only, ciliate on the margin; hypanthium (below the calyx limb) obconical, 2.5–3 mm long; corolla outer surface densely covered with minute short hairs all over, tube cylindrical to slightly inflated just below the mouth, 6–6.5 mm long, inside glabrous, the throat c. 4 mm across but with a highly constricted aperture less than half the throat width due to a pronounced collar-like thickening, lobes 5, narrowly ovate to broad-elliptic, 7–7.5 mm long, inside glabrous; anthers 4–4.5 mm long, with pollen; style 2.5–3 mm long; stigma 4–4.5 mm long; ovary normally developing in the bisexual, failing (unformed) in the male. **Female inflorescence** (not known in the flowering state): peduncle 1–2 mm long, unbranched, with broad-ovate bracts less than 1/3 the length of the flower calyx; flowers 1 per inflorescence, pedicels 1–2 mm long. **Fruit** developing on a stalk 0.3–0.5 cm long, globose to obovoid, 2.2–3.5 cm long, 1.5–2.4 cm wide, glabrous; seeds lens-shaped, rounded to reniform, somewhat compressed, 4–4.5 mm long, 3–3.5 mm wide, testa surface areolate.

DISTRIBUTION. Borneo, known so far only from Central Kalimantan. Lowland mixed dipterocarp forest to *c.* 820 m.

SPECIMENS EXAMINED—BORNEO. KALIMANTAN: C. Kalimantan, headwaters of S. Kahayan, 5 km NW of Tumbang Sian logging camp, 150 m, *Burley, Tukirin et al.* 772, 21 Apr 1988 (holotype SAR! isotypes K! KEP! L! SING!) (flower buds, *M*), 5 km NE of Haruwu village, 820 m, *Burley, Tukirin et al.* 423, 26 Mar 1988 (L!) (fruiting, *F*) & 423A (K! SING!) (fruiting, *F*), 5 km NE of Haruwu village along Miri river, c. 200 m, *Burley, Tukirin et al.* 561, 2 Apr 1988 (K! KEP! L! SING!) (fruiting, *B*).

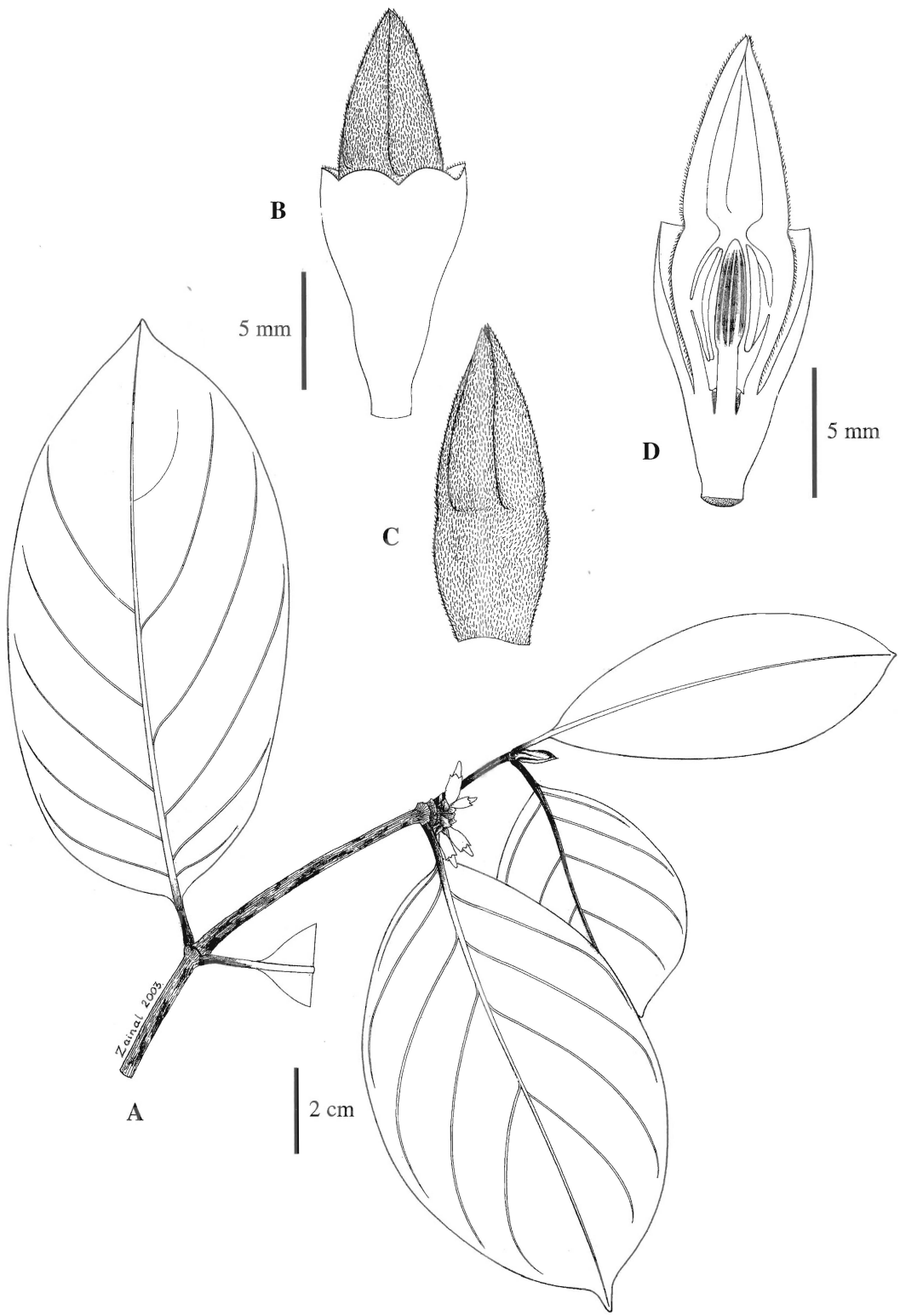

Fig. 4. *Bungarimba kahayanensis*. **A.** Part of leafy branch with male inflorescence. **B.** Male flower bud, general aspect. **C.** Corolla removed from male flower in bud stage. **D.** Longitudinal section through male flower bud (note the hypanthium is totally failing). All from *Burley, Tukirin et al.* 772 (SAR).

2. Bungarimba papuana K.M. Wong, **sp.nov.** *B. sessiliflorae (Ridl.) K.M.Wong similis sed pedicello fructu 1–1.5 cm longo differt. Typus: Ridsdale & Galore NGF 33434, Papua New Guinea, Western District, Kiunga sub-district, Kiunga, c. 200 ft., 21 July 1967 (holotypus SING! isotypi A, CANB, K, L).*

Hemi-epiphyte. **Bark** peeling in small pieces, pale fawn; inner bark red brown. Shoots and leaves glabrous. **Stipules** ovate-lanceolate, free, each with one edge overlapping onto the other, to 0.8 cm long, the whole slightly twisted, glabrous. **Leaves** with petiole 2–2.6 cm long, 1.5–2 mm thick; lamina broad elliptic to slightly obovate, 14–19 cm long, 7–11 cm wide, base cuneate, apex obtuse to cuspidate, coriaceous; midrib on the upper surface slightly prominent, on the lower surface conspicuously prominent; secondary veins 8–10 pairs, slightly prominent on the upper side, prominent on the lower side; tertiary veins indistinct to invisible in the dried leaf. Inflorescences not known but infructescence sessile, branched (probably bisexual). Mature **fruit** on a stalk 1–1.5 cm long, subellipsoid-ovoid, 4.2–4.7 cm long, 2.8–3.3 cm wide, glabrous; seeds lens-shaped to reniform, slightly compressed, 6–9 mm long, 3–5 mm wide, testa surface areolate.

DISTRIBUTION. Only known from Papua New Guinea, in the Western District. Lowland forest on a ridge.

SPECIMENS EXAMINED—PAPUA NEW GUINEA. WESTERN DISTRICT: Kiunga sub-district, Kiunga, *c.* 200 ft., *Ridsdale & Galore* NGF 33434, 21 Jul 1967 (holotype SING! isotypes A, CANB, K, L) (fruits, *B*).

Flowers are unknown for this species and so cannot be compared with those of the other species. However, the mature fruits have distinctly long pedicels, 1–1.5 cm long and none of the other three species have such long fruit pedicels.

3. Bungarimba ridsdalei K.M.Wong, **sp. nov.** *B. sessiliflorae (Ridl.) K.M.Wong similis sed calyce cupulato ore lato, lobis corollae angusti-ovatis vel ellipticis, longioribus dimidii tubi differt. Typus: Aban SAN 56723 Sabah, Ranau, Sosopodon For. Res., 26 April 1968 (holotypus K! isotypi KEP! L, SAN!).*

(Figs. 5 and 6.)

Epiphyte 5 m or more above ground, or (more rarely) ground-rooted hemi-epiphyte with a main stem up to 15 cm diameter, bearing fine adventitious roots all over the stem, and also thick aerial roots descending to the forest floor. **Bark** smooth to narrowly fissured, pale grey-brown. Shoots and leaves glabrous. **Stipules** ovate-lanceolate, free, each with one edge overlapping onto the other, to 1.4 cm long, the whole slightly twisted, glabrous. **Leaves** with petiole 0.7–2 cm long, 2–3 mm thick; lamina narrowly to broad-elliptic, 6.5–18 cm long, 2.5–8.5 cm wide, base cuneate, apex acute to short-acuminate, coriaceous; midrib on the

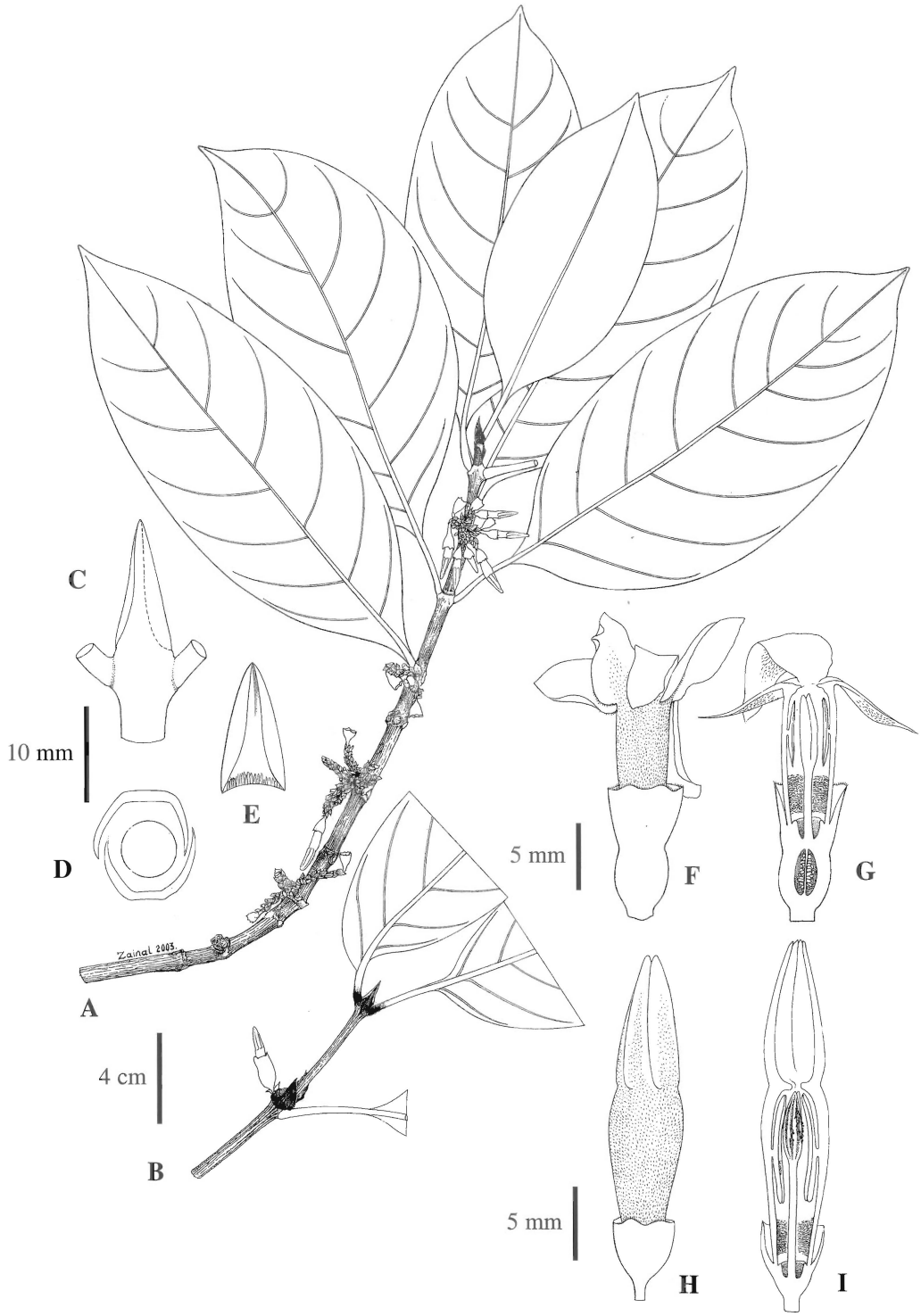

Fig. 5. *Bungarimba ridsdalei*. **A.** Habit, leafy branch with male inflorescences. **B.** Part of branch showing female inflorescence with a solitary flower. **C.** Stipules enclosing terminal bud. **D.** Plan view of stipule positions showing overlapping edges. **E.** View of inner side of one stipule showing a row of colleters at its base. **F.** Female flower, general view. **G.** Longitudinal section of female flower. **H.** Male flower, general view. **I.** Longitudinal section of male flower. A from *Aban* SAN 56723 (K), B from *Beaman* 7917 (K), C–E from *Wong* 2875 (KLU), F-G from *Aban* SAN 50736 (SAN), H–I from *J. & M.S. Clemens* 30867 (L).

upper surface slightly prominent, on the lower surface conspicuously prominent; secondary veins 6–8 pairs, slightly prominent on the upper side, prominent on the lower side; tertiary veins indistinct to invisible in the dried leaf. **Bisexual and male inflorescences**: peduncle 0–1 mm long, compactly branched several to more than 5 times, the main branches subsequently monochasial and subhelicoid with highly condensed internodes and broad-ovate bracts less than 1/3 the length of the flower calyx; flowers typically more than 10 in a cyme, pedicels 1.5–2 mm long, 0.5–1 mm thick; calyx cup-shaped, glabrous outside and inside, lobes 5, rounded, to 0.5 mm high only, ciliate on the margin; hypanthium (below the calyx limb) obconical, 1.5–2 mm long; corolla outer surface with minute short hairs scattered all over or subglabrous, tube cylindrical, 10–12 mm long, inside with a zone of long hairs near the base, the throat 7–8 mm across but with a highly constricted aperture less than half the throat width due to a pronounced collar-like thickening, lobes 5, narrowly ovate to broad-elliptic, 7–8 mm long, inside glabrous; anthers 6.5–7.5 mm long, with pollen; style 7–8 mm long; stigma 4.5–5.5 mm long; ovary normally developing in the bisexual, failing (unformed) in the male. **Female inflorescence**: peduncle 0.5–1mm long, unbranched to sparsely (2–3-)branched, with broad-ovate bracts less than 1/3 the length of the flower calyx; flowers typically 1 (rarely 2) per inflorescence, pedicels 0.5–1.5 mm long, 1–1.5 mm thick; calyx cup-shaped, glabrous outside and inside, lobes 5, rounded, to 0.5 mm high only, ciliate on the margin; hypanthium (below the calyx limb) ellipsoid, 4.5–5 mm long; corolla outer surface with minute short hairs scattered all over or subglabrous, tube cylindrical or slightly inflated below the mouth, 10–11 mm long, inside with a zone of long hairs near the base, the throat 7–8 mm across

Fig. 6. *Bungarimba ridsdalei*, part of plant from which *Wong* 2875 was collected, showing roots growing around its own stem.

but with a highly constricted aperture less than half the throat width due to a pronounced collar-like thickening, lobes 5, narrowly ovate to broad-elliptic, 7–8 mm long, inside glabrous; anthers 5–5.5 mm long, without pollen; style 5–5.5 mm long; stigma 4.5–5 mm long; ovary normally developing. **Fruit** subsessile (the stalk to 0.1 cm long), globose to ellipsoid to obovoid, 1.5–3.2 cm long, 1.2–2.5 cm wide, glabrous; seeds lens-shaped to reniform, somewhat compressed, 4–5 mm long, 3–4 mm wide, testa surface areolate.

DISTRIBUTION. Northwest, north and eastern Borneo (Sarawak, Sabah, Brunei, East Kalimantan). Lower montane forest at 1400–1800 m but sometimes descending to moist valleys in the lowlands (e.g., at Temburong in Brunei Darussalam and the Mulu-Niah area in northern Sarawak). Occurring on various substrates, including sandstone, alluvium and limestone.

SPECIMENS EXAMINED—BORNEO. SABAH: Tenompok, 5000 ft, *Clemens & Clemens* 26335, 7 Sep 1931 (L!) (fruits, *F*), 27652, 22 Dec 1931 (K! L!) (open flowers, flower buds, *M*), 27825, 26 Jan 1932 (L!) (fruits, *B*), 28765, Feb-Mar 1932 (K! L!) (flower buds, *M*, and fruit, *F*, on separate pieces), 28765A, Feb-Mar 1932 (K! flower buds, *M*; L! flower buds, *M*, and fruit, *F*, on separate pieces), 28825, 14 Mar 1932 (L!) (fruits, *F*); Tenompok to Bundu Tuhan forest, 5000 ft, *Aban & Nicholas* SAN 65213, 18 Jan 1969 (K, L, SAN!) (fruits, *F*); Ranau, 5000 ft, mile 35 Ranau road, *Aban* SAN 57792, 15 May 1967 (K! KEP! SAN!) (flower buds, flowers with only calyces left, *M*), 5300 ft, near Kinabalu Nat. Park, *Tarmiji* SAN 75501, 6 Jun 1972 (SAN!) (open flowers, flower buds, *M*); Ranau, Taman Kinabalu, Kiau View, 5100 m, *Amin & Jarius* SAN 117267, 14 Jan 1987 (SAN!) (fruits, *F*); Ranau, Kundasang, *Tikau* SAN 28924, 7 Apr 1962 (KEP! SING!) (fruits, *B*), 4200 ft, *Singh* SAN 27477, 8 Nov 1961 (K, L, SAN! SAR, SING!) (fruits, *F*); Kinabalu Park, behind Rumah Mengilan, *Wong* WKM 2875, 29 Aug 2001 (KLU! SAN! SING!) (fruits, *B*); Mamut, *Aban* SAN 50736, 7 May 1970 (K! SAN! SING!) (flower buds, fruits, *F*) & SAN 66817, 7 May 1970 (SAN!) (open flowers, flower buds, *M*); Sosopodon For. Res., *Aban* SAN 56723, 26 Apr 1968 (holotype K! isotypes KEP! L, SAN) (flower buds, *M*) & SAN 60737, 22 Sep 1967 (K! fruits, *F*; SAN! fruits *B*), 5000 ft, *Battah* SAN 33915, 15 Jul 1963 (K! SAN! SAR) (fruits, *F*), east of Sosopodon For. Res., 4200 ft, *Meijer & Francis* SAN 42759, 16 Feb 1965 (K!) (fruits, *F*) & SAN 42772, 16 Feb 1965 (K! SAN!) (flower buds, *M*); above Sosopodon, 4500 ft, *Mikil* SAN 38661, 13 Jul 1963 (SAN!) (*M* inflorescence fragments); Mt Kinabalu, Pinosuk Plateau, 5000 ft, *Chai & Ilias* RSNB 6032, 7 May 1964 (K! L! SING!) (fruits, *F*); Ranau, trail to Pinosuk plateau, *Aban* SAN 91651, 15 Sep 1979 (SAN!) (fruits, *B*); Kinabalu, Mesilau, 4900 ft, *Sinanggul* SAN 47953, 19 Jan 1965 (SAN!) (fruits, *B*); Kinabalu, Mesilau Cave trail, 4000 ft, *Sadau* SAN 49720, 24 Jul 1965 (SAN!) (fruit, *F*); Mt Kinabalu, Mesilau River, 4500 ft, *Chew & Corner* RSNB 7076, 4 May 1964 (K! L! SAN! SING!) (flower buds, flowers with only calyces left, *M*), 5000 ft, *Chew & Corner* RSNB 4231, 5 Feb 1964 (K! SING!) (fruits, *F*); Mt Kinabalu, Ulu Liwagu and Ulu Mesilau, 4500 ft, *Chew, Corner & Stainton* 2973, 12 Nov 1961 (K! SAN! SING!) (fruits, *F*); Mt Kinabalu, Penibukan, *Clemens & Clemens* 50073, 2 Nov 1933 (K! L!)

(flowers with only calyces left, *M*), 4000 ft, *Clemens & Clemens* 31855, 5 Mar 1933 (K! L!) (flower buds, *M*), 4000-5000 ft, *Clemens & Clemens* 30867, 10 Jan 1933 (L!) (flower buds, *M*), 31102, 16 Jan 1933 (L! SING!) (fruits, *F*), 31274, 1 Feb 1933 (K! L!) (fruits, F), 31436, 7 Feb 1933 (K! L! SING!) (fruits, *F*), 31494, 7 Feb 1933 (BO! K! L!) (fruits, *B*); Mt Kinabalu, Gurulau Spur, 5000 ft, *Clemens & Clemens* 50549, 29 Nov 1933 (L!) (fruits, *F*); Mt Kinabalu, Mahandui river, *c.* 3500 ft, *Carr* SFN 26286, 2 Mar 1933 (SING!) (fruits, *F*); Kota Merudu, west of Bt Madalon, *Aban* SAN 94297, 20 Nov 1981 (SAN!) (fruit, *F*); Tambunan, Crocker Range, 1450 m, *Beaman* 7917, 18 Dec 1983 (K! open flowers, flower buds, *F*; L! fruits, *B*); Penampang, mile 27 ? Crocker Range, 4600 ft, *Chow & Aban* SAN 65453, 13 Oct 1969 (K! SAN!) (flower buds, *M*); Crocker Range F.R., Papar / Keningau road, *Karim* SAN 78425, 20 Feb 1975 (SAN!) (fruit, *F*); Sipitang, SFI, 1370 m, *Maikin et al.* SAN 132825, 17 Jul 1991 (SAN!) (fruits, *B*); Nabawan, Sg. Maadun, *Asik* SAN 118841, 22 May 1987 (K! only *M* flower calyces left; SAN! only *M* and *B* calyces and a fruit left); Lahad Datu, Orchid Plateau, *Kumin* SAN 71092, 25 Jul 1970 (K! SAN!) (fruits, *F*). **SARAWAK:** Lawas, Sg. Belaban, 5500 ft, *Ilias* S.26356, 30 Sep 1967 (SING!) (fruit, *B*); Miri, G. Subis, 400 ft, summit of limestone, *Anderson* S.16047, 6 Jun 1962 (K! L, SAR, SING!) (fruits, *F*); 4th Div., Mulu Nat. Park, Ulu Sg. Berar, 500 ft, *Chai* S.39648, 3 Oct 1977 (K! KEP! L, MO, SAN! SAR) (fruits, *F*), G. Mulu, 4400 ft, *Anderson* 4221, 28 Jun 1961 (K! L! SING!) (flower buds, flowers with only calyces left, *M*); 4th Div., Bario, route to Batu Lawi, 1530 m, *Dy. Awa & Lee* S.50707, 9 Aug 1985 (K! KEP! L! MO, SAN! SAR) (fruits, *B*); 4th Div., Bintulu, Tatau, Sg. Bunut, 500 m, *Ilias* S.50194, 7 Oct 1985 (K, KEP, L, SAN! SAR) fruit, *F*); 4th Div., Bintulu, Tubau, Bt. Sekiwa, 150 m, *Abg. Mohtar et al.* S. 51491, 30 Aug 1986 (K, KEP, L, SAN! SAR) (fruit, *F*) & S.52745, 25 Aug 1986 (K, KEP! L, MO, SAN) (fruit, *B*); 4th Div., Bintulu, Lumut Range, Ulu Sungai Lalang, 280 m, *Julaihi et al.* S.80887, 16 May 1999 (K, KEP! L, SAN! SAR) (fruits, *B*); 7th Div., Kapit, Melinau, Ulu Sampurau, Bt. Salong, 4000 ft, *Ilias* S.25888, 20 Aug 1967 (SING!) (fruit, *B*), Bt. Sampandai, 1600 m, *Ilias* S.40882, 11 Apr 1980 (K! KEP! L, MO, SAN!) (flower buds, *M*), path from Ulu Sampurau to Ulu Melinau, 1400 m, Ilias S.40945, 15 Apr 1980 (K, KEP! L, MO, SAN! SAR) (flower buds, *M*), 7th Div., Kapit, Melinau, *Ilias* S.40949, 14 May 1981 (A, K! KEP! L, MO, SAN, SAR) (fruits, *F*); 7th Div., Kapit, Sut, Sg. Bena, *Ilias* S.41716, 26 Apr 1980 (K, KEP! L, MO, SAN! SAR) (fruit, *F*), S.41720, 26 Apr 1980 (K! KEP! L, MO, SAN) (flower buds, *M*); 7th Div., Kapit, Btg. Balui, Bt. Kumbong, 850 m, *Runi et al.* S.60008, 25 Feb 1992 (K, KEP! L, SAN! SAR) (flower buds, *M*); Bukit Mersing, Anap, basalt ridge, 600 m, *Sibat* S.21899, 22 Aug 1964 (A, BO! K! KEP! L, SAN, SAR! SING!) (fruits, *F*). **BRUNEI:** Temburong, just downstream from K. Belalong, *Wong* WKM 1340, 9 Jul 1989 (BRUN! K! KEP! L! SAN! SING!) (fruits, *F*). **KALIMANTAN:** C. E. Borneo, W. Koetai, near the Kemoel, mountain ridge, *Endert* 4122, 14 Oct 1925 (K! L!) (fruits, *B*), Kemoel, mountain country, *c.* 1800 m, *Endert* 4370, 19 Oct 1925 (K! L!) (fruits, *F*), K. Kemoel, mountain country, 1800 m, *Endert* 4456, 21 Oct 1925 (K! L!) (fruits, *B*).

The species is named after Dr Colin Ridsdale, who carried out much research on the Rubiaceae while based at the Rijksherbarium in Leiden and who has been helpful with my own studies made in this family.

4. Bungarimba sessiliflora (Ridl.) K.M.Wong, **comb. nov.**

Porterandia sessiliflora Ridl., Kew Bulletin (1939) 597; Masamune, Enumeratio Phanerogamarum Bornearum (1942) 703; Wong, Malayan Nature Journal 38 (1984) 46, Tree Flora of Malaya 4 (1989) 393. Typus: *Haviland & Hose*, s.n., 9 Oct. 1894, Sarawak, Kuching "=1961"A (holotypus K!).

(Figs. 7 and 8.)

Tree to 13 m tall, to 15 cm diameter. **Bark** smooth to slightly cracking and dippled, grey-brown. Shoots and leaves glabrous. **Stipules** ovate-lanceolate, free, each with one edge overlapping onto the other, to 1.5 cm long, the whole slightly twisted, glabrous. **Leaves** with petiole 1–2 cm long, 2–3 mm thick; lamina broad-elliptic, 8–19 cm long, 5–11 cm wide, base broad-cuneate to rounded, apex obtuse, coriaceous; midrib on the upper surface slightly prominent, on the lower surface conspicuously prominent; secondary veins 5–8 pairs, slightly prominent on the upper side, prominent on the lower side; tertiary veins invisible in the dried leaf. **Bisexual and male inflorescences**: peduncle 1–2 mm long, compactly branched several to more than 5 times, the main branches subsequently monochasial and sub-helicoid with highly condensed internodes and broad-ovate bracts less than 1/3 the length of the flower calyx; flowers typically more than 10 in a cyme, pedicels 1–1.5 mm long, 1–1.5 mm thick; calyx broad spindle-shaped with a tiny aperture, the limb tearing as the corolla inside expands, glabrous outside and inside, lobes 5, irregularly shaped to rounded, very tiny, 0.1–0.2 mm high only, minutely ciliate on the margin; hypanthium (below the calyx limb) in the male dish-like and 2–2.5 mm long, in the bisexual obconical and 3–3.5 mm long; corolla outer surface completely and densely covered with minute sinuous hairs, tube short-cylindrical, 8–10 mm long, inside with a zone of scattered fine hairs near the base, the throat 4–4.5 mm across but with a highly constricted aperture less than half the throat width due to a pronounced collar-like thickening, lobes 5, broad-ovate to suborbicular, 4–4.5 mm long, inside glabrous; anthers 6–7.5 mm long, with pollen; style 2.5–3 mm long; stigma 7–8 mm long; ovary normally developing in the bisexual, failing (unformed) in the male. **Female inflorescence** (not known in the flowering state): peduncle 2–4 mm long, unbranched, with broad-ovate bracts less than 1/3 the length of the flower calyx; flowers 1 per inflorescence, pedicels 1–2 mm long. **Fruit** developing on a short stalk 0.2–0.5 cm long, subglobose to obovoid, to 2.5–3.4 cm long, to 2.3–2.7 cm wide, glabrous; seeds lens-shaped to reniform, somewhat compressed, 4–6 mm long, 2.5–4 mm wide, testa surface areolate.

DISTRIBUTION. In Borneo, recorded from the Kuching-Bau area of west Sarawak, and in the Sungai Kenepai and Sampit areas in Central Kalimantan. Also Sumatra and Peninsular Malaysia (Perak). Lowland mixed dipterocarp forest and peat swamp forest, also on limestone (in Sarawak).

Although Ridsdale has expressed skepticism that this should be a free-standing tree whereas its congeners in Borneo are clearly epiphytes or hemi-epiphytes, this habit has been

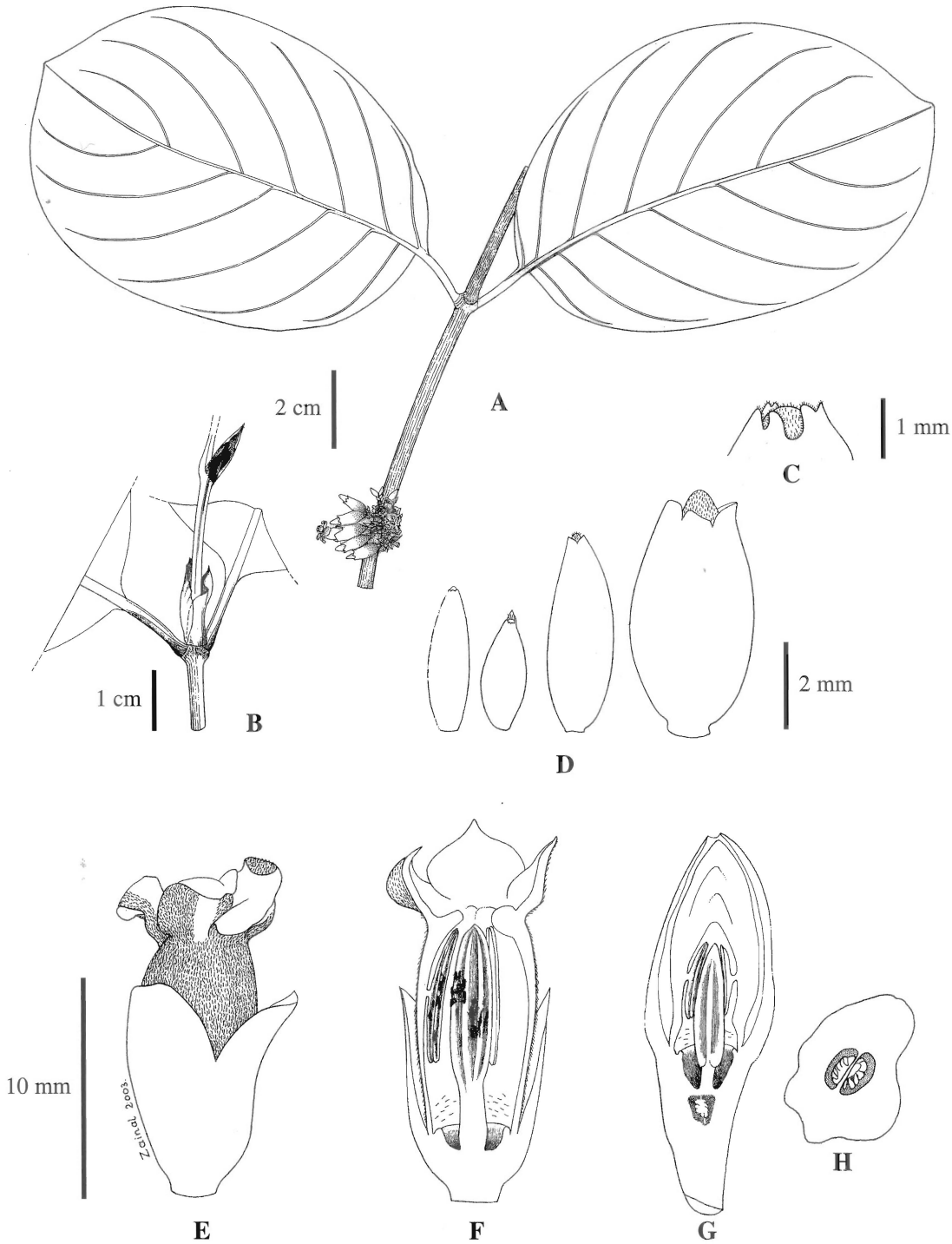

Fig. 7. *Bungarimba sessiliflora*. **A.** Part of leafy branch with male inflorescence. **B.** Stipules at a 2-leaf node. **C.** Summit of young flower bud, showing tiny, irregular calyx lobes and hairy tip of corolla. **D.** Series of four flower buds (progressively older towards the right), showing the tiny aperture of the young calyx (left) and the calyx tearing as the corolla within expands (right). **E.** Mature male flower. **F.** Longitudinal section of male flower (note the hypanthium is totally failing). **G.** Longitudinal section, bisexual flower bud. **H.** Transverse section through ovary of bisexual flower bud. A–F from *Haviland* 134 (L), G–H from *Haviland & Hose*, s.n. 9 Oct. 1894 (K).

Fig. 8. *Bungarimba sessiliflora*, close-up view of male inflorescence showing monochasial main branches with highly condensed internodes. From *Haviland* 134 (L). (Photo: M.S. Zahid)

repeatedly recorded by collectors in the region: "tree 13 m" (*Kostermans* 4654), "tree 30 ft high" (*Muas* S.13366), "tree" (*Patrick* FRI 11137 and *Wong & Kochummen* FRI 32361), "xeropedic —growing on limestone" (*Sie* S.43892).

SPECIMENS EXAMINED—SUMATRA. INDRAGIRI: Sungei Laloh, *Curtis* 3543, Jan 1901 (K! SING!) (fruiting, *F*). **MALAY PENINSULA. PERAK:** G. Bubu Res., *Patrick* FRI 11137, 17 Jun 1969 (K! KEP! L) (fruiting, *F*); Kledang Saiong, *Wong & Kochummen* FRI 32361, 23 Feb 1982 (KEP!) (fruiting, *F*). **BORNEO. SARAWAK:** Kuching, *Haviland & Hose*, s.n., 9 Oct. 1894 (=1961)A (holotype K!) (open flowers and fruiting, *B*) & s.n., 31 Oct. 1894 (=1961)Z (K!) (open flowers, *M*), *Haviland* 134 (=1961)B, 1893 (L! SING!) (open flowers, *M*); Bau, Jambusan, *Sie* S.43892, 18 Nov. 1981 (K! L, SAN! SAR) (open flowers, *M*); Bau, foot of Fairy Cave, limestone, Jamree et al. S. 82061, 9 Feb 1999 (K, KEP! SAR) (fruiting, *F*); Serian, Sg. Ensebang, Balai Ringin P.F., *Muas* S.13366, 23 Mar 1961 (A, K, L!, SAR!, SING!) (fruiting, *F*). **KALIMANTAN:** West Kalimantan, Soengai Kenepai, *Hallier* 2001, 1893-94 (L!) (remains of inflorescence bases and fruit, *B*) & 2095, 1893-94 (BO!) (*X*); C. Kalimantan, Sampit region, *Kostermans* 4654, 8 Apr 1948, "paka bawi" (BO! K! L! SING!) (fruiting, *F*).

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